EXCLUSIVE PREFERENCE DEVELOPS LESS READILY ON CONCURRENT RATIO SCHEDULES WITH WHEEL-RUNNING THAN WITH SUCROSE REINFORCEMENT

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Previous research suggested that allocation of responses on concurrent schedules of wheel-running reinforcement was less sensitive to schedule differences than typically observed with more conventional reinforcers. To assess this possibility, 16 female Long Evans rats were exposed to concurrent FR FR schedules of reinforcement and the schedule value on one alternative was systematically increased. In one condition, the reinforcer on both alternatives was .1 ml of 7.5% sucrose solution; in the other, it was a 30-s opportunity to run in a wheel. Results showed that the average ratio at which greater than 90% of responses were allocated to the unchanged alternative was higher with wheel-running reinforcement. As the ratio requirement was initially increased, responding strongly shifted toward the unchanged alternative with sucrose, but not with wheel running. Instead, responding initially increased on both alternatives, then subsequently shifted toward the unchanged alternative. Furthermore, changeover responses as a percentage of total responses decreased with sucrose, but not wheel-running reinforcement. Finally, for some animals, responding on the increasing ratio alternative decreased as the ratio requirement increased, but then stopped and did not decline with further increments. The implications of these results for theories of choice are discussed.

Key words: concurrent ratio schedules, wheel-running reinforcement, sucrose reinforcement, lever press, rat

In their investigation of the opportunity to run in a wheel as a reinforcing consequence for lever pressing on fixed-ratio schedules, Collier and Hirsch (1971) concluded that wheel running produced results "similar in all respects to those reported when food or water are used as reinforcers for ratio schedules" (p. 159). Subsequent investigations, however, suggest that the conclusion that running generates schedule effects similar to those with more conventional reinforcers was premature. Running generates longer postreinforcement pause (PRP) durations and lower response rates than typically observed with more conventional reinforcers (Belke, 1998, 2000a, 2004, 2006a; Belke, Pierce, & Duncan, 2006). The basis for these longer PRPs and their potential to interact with reinforcement schedules remains to be determined. Furthermore, lever-pressing rates may vary as a function of changes in wheel-running rates within a session (Belke, 2000b).

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More recently, the investigation of the properties of wheel-running reinforcement was extended to concurrent schedules of reinforcement. Belke and Belliveau (2001) investigated choice between alternatives providing wheel-running reinforcement on concurrent variable-interval (VI) schedules when relative rates of reinforcement were varied. The reinforcer on both alternatives was the opportunity to run for 15 s. Matching law analyses revealed mean slopes for time and response allocation of 0.82 and 0.60. While the slope for time allocation was similar to that observed with more conventional reinforcers (e.g., food; see Baum, 1979), the slope for response allocation was much lower. Belke and Belliveau suggested that the lower sensitivity for responses was due to a low response rate, high changeover rate, and long postreinforcement pauses. In terms of the first two factors, a low response rate and high rate of changeovers, the investigators noted that changeover responses constituted one fourth to one third of all responses. When response allocation was corrected by removing changeover responses, the mean slope for response allocation increased to 0.84. With respect to the third factor, the authors noted that long pauses might also have produced the lower sensitivity for response allocation; however, there was no

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way to correct for this factor since postreinforcement pauses were not measured.

Belke et al. (2006) exposed rats to the same series of concurrent variable-ratio (VR) schedules with wheel-running reinforcement on both alternatives, sucrose reinforcement on both alternatives, and wheel running on one alternative and sucrose on the other. Rats were exposed to conc VR 10 VR 10, conc VR 5 VR 20, and conc VR 20 VR 5 schedules with each set of reinforcers. Across these three schedule pairs, with wheel running as the reinforcer on both alternatives, mean response proportions on an alternative were 0.42, 0.28, and 0.74; with sucrose as the reinforcer on both alternatives, the equivalent values were 0.43, 0.22, and 0.79. Analysis of the differences showed that the shifts in preference in response to the changes in ratio requirements were greater with sucrose as the reinforcer. This led to the anomalous conclusion from a behavioral economic analysis that sucrose is a better substitute for sucrose than is wheel running for wheel running.

In addition, as observed by Belke and Belliveau (2001), changeovers constituted a substantial percentage of the total responses when wheel running was the reinforcer on both alternatives. Across the conc VR 10 VR 10, conc VR 5 VR 20, and conc VR 20 VR 5 conditions, 28.7, 29.2, and 29.4% of responses were changeover responses. In contrast, with sucrose solution on both alternatives, the equivalent percentages were 16.0, 12.0, and 12.4%. When the reinforcers on each alternative differed, the equivalent percentages were 29.0% (Sucrose VR 10 – Wheel VR 10), 19.3% (Sucrose VR 5 – Wheel VR 20), and 27.2% (Sucrose VR 20 – Wheel VR 5). When the response requirement for sucrose decreased to VR 5, 65% of responses were allocated to this alternative and the percentage of responses that were changeovers decreased. In contrast, when the response requirement for wheel running decreased to VR 5, only 50% of responses were allocated to the wheel-running alternative and the percentage of responses that were changeovers remained relatively unchanged.

Since rate of changeovers is related to sensitivity to the difference in reinforcement contingencies between alternatives (Baum, 1974, 1979), these data suggest that rats may be less sensitive to differences between rein-

forcement schedules on concurrent schedules when the reinforcer is wheel running. One possibility, according to the contingency discriminability model (Davison & Jenkins, 1985) is that rats less accurately attribute reinforcers to response alternatives when wheel running is the reinforcer and this confusion affects response allocation. The model is specified by the following equation (Jones & Davison, 1998):

$$B_1/B_2 = c(R_1 - p R_1 + R_2)/(R_2 - p R_2 + R_1)$$
 (1)

 B_1 and B_2 represent behavior allocated to two alternative sources of reinforcement, respectively. R₁ and R₂ represent reinforcers obtained from these alternatives. Bias toward one alternative based on a factor other than the relative rate of reinforcement is represented by c and the parameter p is an index of "proportional confusion (the inverse of discriminability) between the two reinforcer contingencies" (Davison & Jones, 1995, p. 148). The value of p varies between 0 (no confusion) and .5 (complete confusion). According to Davison and Jenkins, the contingency discriminability model describes behavior allocation on concurrent interval schedules as well as, if not better than, the generalized matching law (Baum, 1974) and provides an explanation for deviations from strict matching (i.e., undermatching, overmatching).

The higher percentage of total responses that are changeovers when wheel running is the reinforcer could be a product of this inaccurate attribution of reinforcers to their respective alternatives. In addition, although the mechanism is not clear, the longer reinforcer duration and postreinforcement pause duration associated with wheel running may also contribute to reduced contingency discriminability. Jones and Davison (1998) showed that discriminability of a response-reinforcer relation decreased as the time since a changeover increased. This effect illustrates that discriminability can be affected by temporal factors.

Killeen and Smith (1984) proposed a related account that does explain how the longer wheel-running reinforcer duration could lead to misattribution of a reinforcer to a response alternative. In an experiment where pigeons had to discriminate whether the delivery of food was dependent on, or

independent of, their behavior, as the duration of the food reinforcer increased from 1 to 4 s, accuracy deteriorated from 0.8 at 1 s to almost 0.5 (i.e., chance) at 4 s. In a comparison condition, where the duration of illumination of a hopper light was varied from 1 to 4 s, accuracy only decreased from 0.8 to about 0.73. According to Killeen and Smith, time spent consuming the reinforcer had a memory erasure effect that reduced the pigeon's ability to report on the source of the food. If time spent running is akin to time spent consuming food with respect to this effect, then the longer duration during which the rats are running would lead them to less accurately attribute a reinforcer to the correct alternative. Belke (2006b) suggested that this may account for why rats fail to show a preference for a longer (i.e., 50 s) over a shorter (i.e., 10 s) wheelrunning reinforcer.

A third possibility for a lack of sensitivity to differences in reinforcement schedules is the low apparent value of an opportunity to run as a reinforcer. Belke et al. (2006) showed that on concurrent VI schedules, rats were indifferent between a 30-s opportunity to run and a drop of 2.5% sucrose solution. Consistent with this, Belke and Hancock (2003) showed that on fixed interval (FI) 30-s schedules, a 15-s opportunity to run produced a response rate function roughly equivalent to that produced by a drop of 2.5% sucrose solution. If sensitivity to differences in reinforcement schedules is affected by the value of the reinforcers, then at low values, rats may be less sensitive than at higher values.

In the current study, sensitivity to differences in reinforcement schedules as a function of reinforcer type was investigated by exposing rats to concurrent ratio schedules in which the response requirement for a reinforcer was initially low (i.e., FR 4) on both alternatives and then the response requirement on the initially preferred alternative was systematically increased (i.e., 6, 8, 12, 16, 24, 32, 40, 56, 72, and 88 responses). As the response requirement increased, one would predict that the rats should rapidly shift exclusively or nearly exclusively to the alternative with the unchanged schedule requirement. This procedure was carried out with wheel running as the reinforcer on both alternatives and with sucrose as the reinforcer on both alternatives.

When Petry and Heyman (1995) used this procedure with concurrent VR schedules and sucrose reinforcement, they found that all rats switched almost exclusively to the unchanged alternative (i.e., VR 8) when the ratio requirement on the other alternative was increased by a factor of 1.75 (i.e., VR 14). On average, the switch occurred when the ratio requirement on the more expensive alternative was 1.5 times (i.e., VR 12) that of the cheaper alternative. When Herrnstein and Loveland (1975) used this procedure with VR schedules and food reinforcement, pigeons demonstrated exclusive preference for the lower ratio alternative when schedules differed by approximately 2:1 (e.g., 40:20) when the ratio values on both alternatives summed to 60 and closer to 4:1 (e.g., 96:24) when they summed to 120.

METHOD

Subjects

Sixteen female Long Evans rats obtained from Charles River Laboratories in St Constant, Quebec served as subjects. The rats were not experimentally naïve—they were exposed to basic classical and operant conditioning techniques in laboratory exercises in a conditioning course and then subsequently participated in an operant investigation of wheelrunning reinforcement. At the point where the animals commenced the first condition of this study, the animals were approximately 1.5 years old. The rats were housed individually in polycarbonate cages (480 mm long by 270 mm wide by 220 mm high) in a holding room on a 12 hr light/dark cycle, with the lights coming on at 0730. Distilled water was available at all times in the home cage. The rats were maintained at a target weight approximately 85% of a free-feeding body weight taken when the rats' weight exceeded 300 grams (i.e., adult weight). Target weights varied around 260 + / - 10 g.

Apparatus

Four activity wheels were used for the experimental sessions; two Wahmann (355 mm in diameter) and two Lafayette Instruments (350 mm in diameter) activity wheels. All wheels were located in sound-attenuating shells equipped with fans to mask extraneous noise and to provide ventilation. A solenoid-

operated brake was attached to the base of each wheel. When the solenoid was operated, a rubber tip attached to a metal shaft contacted the outer rim of the wheel and brought the wheel to a stop. Two 24-VDC lights mounted on the wheel frame served to illuminate the interior of the wheel chamber. Revolutions were recorded by a microswitch attached to the wheel frame.

A Plexiglas panel (162 mm high by 181 mm wide by 5 mm thick) that held two response levers, two stimulus lights, and a solution receptacle was attached to each wheel frame by Velcro. The levers were 15 mm wide, 45 mm apart, and extended 20 mm beyond the surface of the panel. They were located 119 mm from the base of the panel and required between 0.3 and 0.4 N of force to close the microswitch. Levers were paired according to the force requirement to reduce response bias. A solution receptacle (38 mm by 31 mm by 61 mm) was located in the space between the two levers. Sucrose solution was contained in a cylindrical dispenser and delivered into the receptacle via a solenoid valve controlled by a Lafayette Instruments Co. Model 80201 liquid dispenser. Sucrose dispensers were 38 mm in diameter, 108 mm long, and held in place by a metal clamp above the receptacle. When the panel was attached to the wheel, the levers extended through an opening (70 mm by 90 mm) and were 75 mm above the floor of the wheel. Yellow LED lights (3 mm in diameter) were located 7 mm above each lever. Control of experimental events and recording of data were handled by a Borland Turbo Pascal 4.0 program run on IBM PC computers interfaced to the wheel through the parallel port.

Procedure

Initial Training. Training the animals to press for the opportunity to run in a wheel occurred in a different set of running wheels equipped with retractable levers (MED Associates ENV-112), a solenoid-operated brake, and 24-VDC lights. In this phase, rats were given the opportunity to run for 30 min each day. After 30 sessions, the opportunity to run for 60 s was made contingent upon a single press (FR 1) of the retractable lever. A lever press caused the lever to retract and the brake to release. The wheel was free to turn for 60 s. After 60 s the brake was engaged and the

retractable lever extended. A session terminated when 30 reinforcers were obtained. This schedule remained in effect for 6 sessions. Following this, the rats experienced VR 3, VR 5, and VR 9 schedules for 6, 8, and 10 sessions, respectively. Upon completion of these sessions, the rats were placed on an FR schedule of wheel-running reinforcement to participate in another experiment.

Training on concurrent schedules. Following completion of this other experiment, the rats were trained for responding on concurrent schedules by first being exposed to concurrent VR 5 VR 5 schedules with the reinforcer on each alternative being the opportunity to run for 20 revolutions. When the schedules were in effect, the yellow LED stimulus lights over the lever were illuminated and the brake was engaged. Each lever press extinguished the LED stimulus light above it for .08 s. When the schedule requirement on either alternative was met, the yellow LED stimulus lights were extinguished, the brake was disengaged, and the 24-VDC lights on the sides of the wheel frame were illuminated. When 20 revolutions had occurred, the 24-VDC side lights were extinguished, the brake was engaged, and the yellow LED stimulus lights were illuminated. Sessions ended when the rats had allocated 150 lever presses between the alternatives. Rats remained on this schedule for 20 sessions.

The rats were then exposed to concurrent FR 4 FR 4 schedules with the opportunity to run for 30 s as the reinforcer on each alternative for 20 sessions. The stimulus conditions were the same as described above. Sessions ended after 1 hr. Initial side preferences were determined as the alternative with the greater average number of responses over the last five sessions. These preferences were used to determine the alternatives on which the ratio would remain constant and on which the ratio requirement would be systematically incremented. The alternative that was initially preferred determined the alternative on which the ratio requirement would be raised. Based on this determination the left alternative was incremented for 10 rats (ND 2, 3, 5, 8, 9, 13, 15, 17, 18, and 19) and the right for 6 rats (ND 7, 10, 11, 14, 16, and 21).

At this point, half the rats were selected to begin responding on concurrent FR 4 FR 4 schedules with 0.1 ml of 7.5% sucrose as the reinforcer on each alternative while the other

half would have a 30-s opportunity to run as the reinforcer on each alternative. Rats ND 5, 7, 8, 10, 14, 16, 17, and 19 began with sucrose while ND 2, 3, 9, 11, 13, 15, 18, and 21 began with wheel running. With sucrose reinforcement, the stimulus conditions were the same as described previously except that when a drop of sucrose solution was delivered the brake remained engaged and the lights at the side of the wheel remained on for 2.5 s to allow time for consumption. After 2.5 s elapsed, the side lights were extinguished and the yellow LED stimulus lights over the levers were illuminated to signal that the reinforcement schedule was in operation. To accommodate the difference in reinforcer durations, the duration of a session was 1 hr when the reinforcer was wheel running and 15 min when the reinforcer was sucrose. Wheel-running and sucrose reinforcement were assigned so that within each of the four running wheels, 2 rats were exposed to the reinforcer types in the wheel running then sucrose order and 2 were exposed to the reverse order.

Between exposures to each type of reinforcer, rats were exposed to concurrent FR 4 FR 4 schedules of wheel-running and sucrose reinforcement with a budget of 120 presses. The schedule was programmed so that sucrose reinforcement would occur on the increasing ratio requirement alternative from the previous series when the previous series involved wheelrunning reinforcement, and that wheel-running reinforcement would occur on the constant ratio requirement alternative from the previous series when that series involved sucrose reinforcement. In other words, the tendency for rats to shift responding toward sucrose in preference to wheel running was used to break down the preference for an alternative that would have developed for the constant ratio requirement alternative. This schedule remained in effect until the preference showed signs of breaking toward indifference. Once the established preference showed signs of breaking down (e.g., decreased to between .50 and .60, approximately), the animal was exposed to the concurrent FR 4 FR 4 schedules with the other type of reinforcer available on both alternatives (i.e., if a rat completed a series with sucrose on both reinforcers, then once the established preference broke, the animal began the next series with wheel running on both alternatives).

Starting with concurrent FR 4 FR 4 schedules with each reinforcer type, the schedule on the increasing ratio alternative was increased across values of 6, 8, 12, 16, 24, 32, 40, 56, 72, and 88 responses. Increments were smaller initially because of the expectation that the shift toward near-exclusive preference would occur when there was a relatively small difference between the schedule requirements. Near-exclusive preference was defined as a response allocation on the alternative with the lower response requirement greater than 90%. A schedule requirement was changed when the following three criteria were met. First, the animal had to complete a minimum of eight sessions under a given requirement. Second, response rates within the last three sessions on both alternatives could not be lower or higher than those which had occurred on that alternative over all previous sessions on that schedule pair (i.e., no new low or high values). Third, there could be no trend in the response rates on either alternative. The ratio requirement with each reinforcer type was increased until the response allocation on the alternative where the response requirement remained FR 4 was greater than 90% in each of the three sessions that met the stability requirement or until stability at the highest ratio requirement had occurred without producing near exclusive preference for the unchanged alternative.

Dependent measures. Lever presses, time spent on, changeovers to, and reinforcers obtained from each alternative were recorded during each session, as well as number of wheel revolutions. Time on an alternative was defined by changeovers; that is, an animal was considered being on an alternative, and time was accumulated, until a response was made on the other alternative. Time taken to complete a session was also recorded.

RESULTS

Figure 1 shows the distribution of ratio values at which the criterion of 90% of responses on the unchanged ratio alternative was met when the reinforcers were wheel running and sucrose with some exceptions. First, ND 15 died suddenly before completing the first series with wheel-running reinforcement and was not included in the analyses. Second, although ND 5 did not complete the

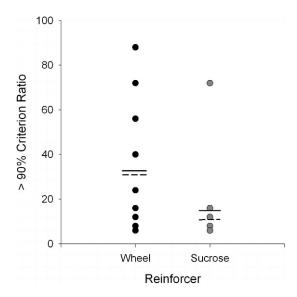


Fig. 1. Ratio values that met the criterion of > 90% of responses on the constant ratio alternative when the reinforcers were wheel running and when they were sucrose for each rat. Note that in cases where the rat did not meet this criterion, the highest ratio value was used. The solid and broken lines represent the mean values with the data from the rat that produced the outlier value in the sucrose distribution included and excluded, respectively.

wheel-running series, her last completed value on this series was greater than the value completed for sucrose; consequently, it was included in the distribution of values for wheel running. Third, with respect to ND 10 and ND 18, the final ratio value of 88 was included in the wheel-running distribution even though the 90% criterion had not been met by this ratio. Finally, the data value for ND 14 was an outlier (> 3 S.D. above the mean) in the sucrose distribution. Means were calculated and analyses conducted with the data values for this rat included and excluded. Data for this and all subsequent analyses are provided in the Appendix.

Mean ratios for wheel running and sucrose with ND 14 included were 32.6 and 15.1, respectively; with ND 14 excluded, 31.0 and 11.0, respectively. Paired t-test comparisons revealed that the ratio required to meet the 90% requirement was significantly lower when the reinforcer was sucrose, with ND 14 included, t(14) = 2.28, p = .04, two-tailed, and with ND 14 excluded, t(13) = 2.54, p = .02, two-tailed.

Although the order of exposure to the different reinforcer types was approximately counterbalanced across the two series, it is possible that rats could achieve the criterion at a lower ratio on the second exposure regardless of type of reinforcer. If there was no difference between the two reinforcers in terms of obtained criterion values, then an effect of repeated exposure, if one occurred, could be observed. In contrast, if, as hypothesized, the criterion value for sucrose would be lower, then a lower criterion value should be more likely for rats exposed to wheel running first, but less likely for those exposed to sucrose first. Evidence consistent with this hypothesis would mitigate against an order effect. Analysis showed that criterion values from first exposure (M = 26.3 responses) were not significantly greater than those for second exposure (M = 21.5 responses), t(14) = 0.54.

Figures 2 and 3 show the percentage of responses on the increasing ratio alternative as a function of the fixed-ratio requirement on that alternative for wheel running and sucrose for different subsets of the rats. The dotted line represents the point at which 90% of responses were allocated on the constant ratio alternative. Visual inspection of these figures reveals the different patterns of changes in relative responses on this alternative across the different reinforcer types. For ND 2, 14, and 17 the values that met the criterion were higher for sucrose. Response allocation on this alternative decreased more rapidly with wheel running as the reinforcer for these rats. For ND 7, 8, and 13 the values that met the criterion were equivalent for both reinforcer types. Response allocation declined similarly with both reinforcers for ND 7 and ND 13; however, for ND 8, response allocation with wheel running did not systematically decline. Finally, for ND 3, 5, 9, 10, 11, 16, 18, 19, and 21 the values that met the criterion were higher for wheel running. Of the rats in this last grouping, several observations can be made. For ND 9, response allocation to this alternative decreased more slowly when wheel running was the reinforcer. For ND 3, 11, and 16, response allocation initially increased then decreased when wheel running was the reinforcer, but only decreased when sucrose was the reinforcer. For ND 10, 18, and 19, response allocation to this alternative decreased initially, but then slowed in its decline as the ratio requirement further increased. In contrast, response allocation when sucrose was the reinforcer declined as the ratio initially

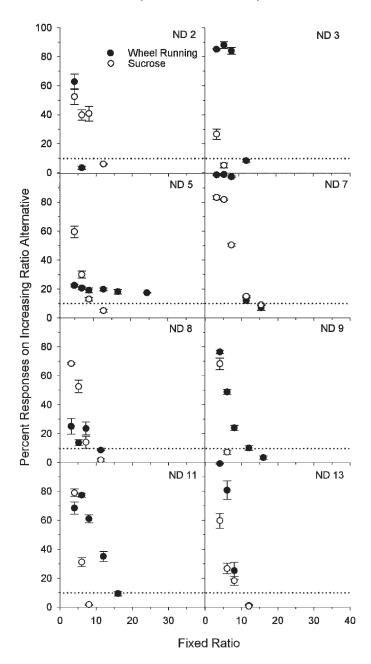


Fig. 2. Percent of responses allocated to the increasing ratio alternative when wheel running (filled circles) and sucrose (unfilled circles) were the reinforcers for rats ND 2, 3, 5, 7, 8, 9, 11, and 13. The dotted line represents the point at which the series of increasing ratio requirements would be terminated because more than 90% of responses would be allocated to the constant ratio alternative.

increased. For ND 21, response allocation to this alternative did not change with the initial increase in the ratio requirement, but then declined. Finally, ND 5 showed little change in response allocation over the ratios completed when wheel running was the reinforcer, but

showed a marked decline in allocation when sucrose was the reinforcer.

Figures 4 and 5 show total responses allocated to both alternatives, responses allocated to the constant ratio alternative, and responses allocated to the increasing ratio alternative

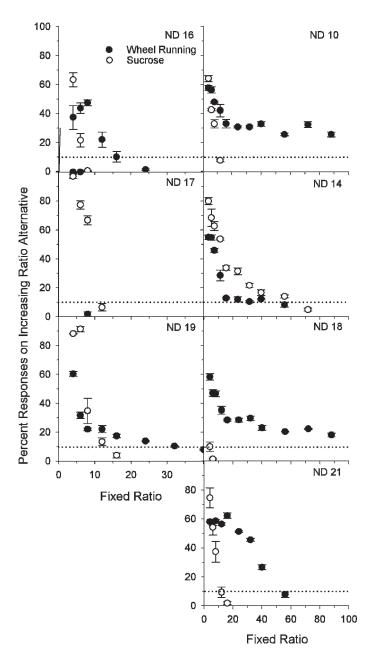


Fig. 3. Percent of responses allocated to the increasing ratio alternative when wheel running (filled circles) and sucrose (unfilled circles) were the reinforcers for rats ND 10, 14, 16, 17, 18, 19, and 21. Note that the scale on the abscissa is different for ND 10, 14, 18, and 21 because the data for these rats were extended over a much greater range than that for the other rats. The dotted line in each graph represents the point at which the series of increasing ratio requirements would be terminated because more than 90% of responses would be allocated to the constant ratio alternative.

with wheel running as the reinforcer for different subsets of the rats. The changes in response allocation depicted in Figures 2 and 3 might reflect reallocation of responses to the constant ratio alternative as the ratio requirement on the other alternative increased. This assumes that total responses remained constant and that reallocation was the only process occurring. However, if total responses increased, then the additional responses could

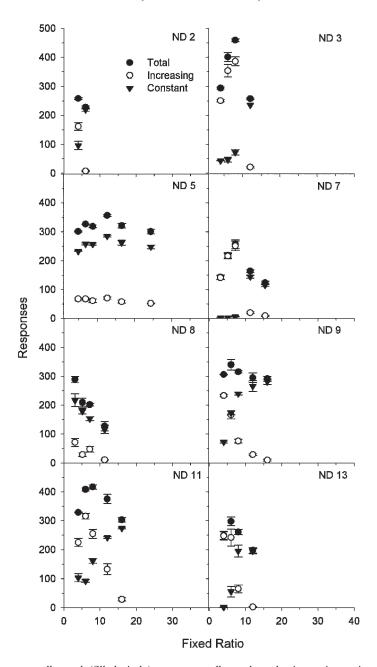


Fig. 4. Total responses allocated (filled circle), responses allocated to the increasing ratio alternative (unfilled circle), and responses allocated to the constant ratio alternative (inverted filled triangle) when the reinforcer was wheel running for rats ND 2, 3, 5, 7, 8, 9, 11, and 13.

be allocated to the constant alternative, the increasing ratio alternative, or both. If they are allocated to the increasing ratio alternative then this would counter the effects of reallocation. Visual inspection of the figures shows that, in general, total responses (filled

circles) increased as the ratio requirement was initially being increased then decreased. This pattern of changes is clearly evident for 12 of 15 rats. For ND 2, 8, and 17, total responses decreased as the ratio requirement increased.

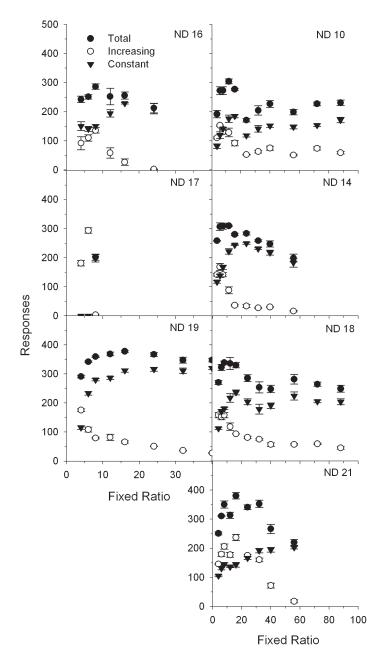


Fig. 5. Total responses allocated (filled circle), responses allocated to the increasing ratio alternative (unfilled circle), and responses allocated to the constant ratio alternative (inverted filled triangle) when the reinforcer was wheel running for rats ND 10, 14, 16, 17, 18, 19, and 21. Note that the scale on the abscissa is different for ND 10, 14, 18, and 21 because the data for these rats were extended over a much greater range than that for the other rats.

With respect to the increasing ratio alternative (unfilled circles), responses allocated to this alternative showed a similar pattern—increased then decreased as the ratio requirement increased. Specifically, ND 3, 7, 10, 11, 14, 16, 17, 18, and 21 showed initial increases

followed by decreases. In contrast, for ND 2, 8, 9, 13, and 19, responses on the increasing rate alternative decreased as the ratio requirement increased. For ND 5 allocation to this alternative remained relatively constant as the ratio requirement increased.

With respect to the constant ratio requirement alternative (triangles), as would be expected, with the exception of ND 8, responding on this alternative generally increased as the ratio requirement increased across all rats. The rats differed with respect to how rapidly allocation to this alternative increased and at what ratio responses allocated to this alternative constituted total responses or nearly all the responses allocated. For rats ND 5, 10, and 18, responses to this alternative never constituted total responses allocated, because a substantial number of responses continued to be allocated to the increasing ratio alternative. For ND 8, allocation to this alternative decreased as the requirement on the increasing ratio alternative increased; however, this change occurred in conjunction with a decline in total responses.

Figures 6 and 7 depict total responses allocated to both alternatives, responses allocated to the constant ratio alternative, and responses allocated to the increasing ratio alternative with sucrose reinforcers for different subsets of the rats. Unlike the previous set of figures, this set shows that as the ratio requirement increased, responses quickly shifted away from the increasing ratio alternative toward the constant ratio alternative for 14 of 15 rats (the exception being ND 14). With respect to total responses allocated, as with wheel running there was an increase in total responses as the ratio requirement increased. With the exception of ND 18, all rats showed some increase in total responses with the initial increments in the ratio requirement. For some rats (ND 2, 7, 8, 14, 17, 19, and 21), this initial increase was followed by a decrease. ND 14 showed an increase followed by a decrease followed by an increase as the ratio requirement increased.

With respect to the increasing ratio alternative, response allocation declined as the ratio requirement increased for 11 of 15 rats. Only ND 7 and 19 showed an initial increase followed by a decrease. Rat ND 2 showed no change followed by a decline in responses as the ratio requirement increased. ND 14 showed a slower decline in responses allocated to this alternative.

With respect to the constant ratio alternative, responses allocated to this alternative increased rapidly as the ratio requirement increased for 13 of 15 rats. Response allocation to this alternative also increased for ND 21,

although less rapidly than for the other rats. For ND 18, responses to this alternative were close to the total number of responses and did not change. Instead, total responses decreased and responses on the increasing ratio alternative decreased so that responses on the constant ratio alternative constituted total responses.

Figures 8 and 9 show the total number of changeovers expressed as a percent of total responses for sucrose and wheel-running reinforcement for different subsets of the rats. Visual inspection of these figures suggests that for sucrose, changeovers as a percent of total responses decreased rapidly as the ratio requirement increased for 12 of 15 rats. For rat ND 7, changeovers as a percent of total responses did not decrease while for ND 14 and 17, changeovers increased then decreased. In contrast, for wheel running, the patterns of change were different. For ND 5, 7, 8, 10, 11, 13, and 21 changeovers as a percent of total responses increased or did not change across initial increments in the ratio requirement. For ND 2, 9, 14, 16, 18, and 19 changeovers as a percent of total responses decreased, although less rapidly than they did for sucrose.

Table 1 shows overall response rates (presses/min), local response rates (presses/min), mean postreinforcement pause durations (s) and changeover rates (changeovers/min) from the initial equal FR 4 ratio conditions with wheel-running and sucrose reinforcement for each rat. Overall response rates were calculated as lever presses on an alternative divided by time spent lever pressing plus postreinforcement pause duration. Local response rates were calculated as lever presses on an alternative divided by time spent lever pressing on an alternative divided by time spent lever pressing on an alternative.

Mean overall rates for sucrose and wheel-running reinforcement were 43.8 and 9.8 presses per min, respectively. A paired t-test comparison revealed that overall response rates generated by sucrose were greater than those generated by wheel running, t(14) = -4.85, p < .001. Similarly, sucrose generated a higher local response rate, t(14) = -3.08, p < .01. Mean local response rates for sucrose and wheel-running reinforcement were 138.8 and 75.5 responses per min, respectively. Sucrose also produced a shorter mean PRP than wheel running, t(14) = 5.52, p < .001. Mean postreinforcement pauses for sucrose and

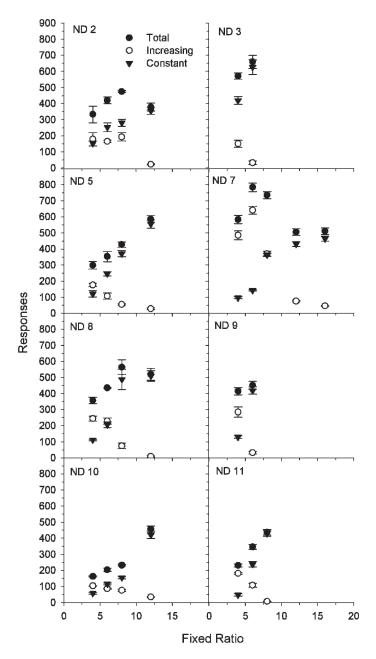


Fig. 6. Total responses allocated (filled circle), responses allocated to the increasing ratio alternative (unfilled circle), and responses allocated to the constant ratio alternative (inverted filled triangle) when the reinforcer was sucrose for rats ND 2, 3, 5, 7, 8, 9, 10, and 11.

wheel running were 4.7 s and 24.2 s, respectively.

Changeovers as a percent of total responses can vary as a function of changeover rate or total responses. That is, if wheel-running reinforcement engenders a higher rate of switching between alternatives than does sucrose, then given equivalent total responses, the percentage of total responses that are changeovers would be higher for wheel running. Alternatively, if wheel-running and sucrose reinforcement did not differ with respect

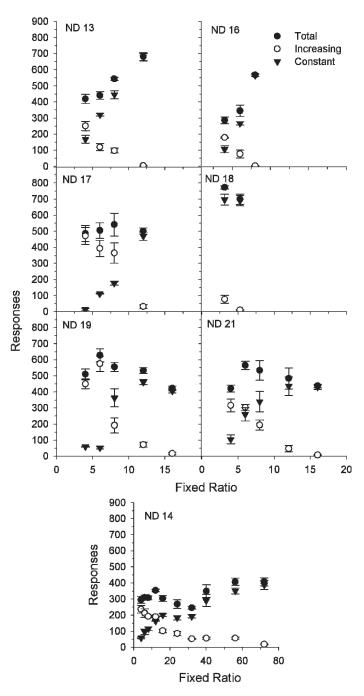


Fig. 7. Total responses allocated (filled circle), responses allocated to the increasing ratio alternative (unfilled circle), and responses allocated to the constant ratio alternative (inverted filled triangle) when the reinforcer was sucrose for rats ND 13, 14, 16, 17, 18, 19, and 21. Note that the scale on the abscissa is different for ND 14 because the data for this rat were extended over a much greater range than that for the other rats.

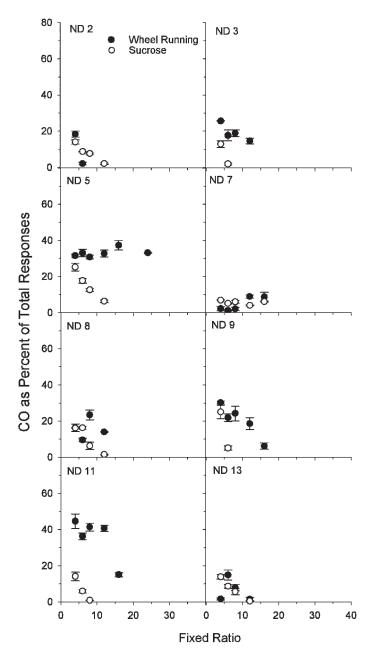


Fig. 8. Changeovers as a percentage of total responses as a function of fixed ratio schedule value for wheel running (filled circles) and sucrose (unfilled circles) reinforcement for rats ND 2, 3, 5, 7, 8, 9, 11, and 13.

to the rate of switching, then changeovers would only constitute a higher percentage of total responses with wheel running as the reinforcer if wheel running generated fewer total responses than sucrose. Table 1 suggests that the latter is the case. Mean rates of changeovers with wheel-running and sucrose

reinforcement were 17.1 and 17.9 changeovers/min, respectively. A paired t-test revealed no significant difference in the rate of changeovers occurring when wheel running and sucrose were the reinforcers, t(14) =-0.3. With respect to previous reports that changeovers constitute a higher percentage of

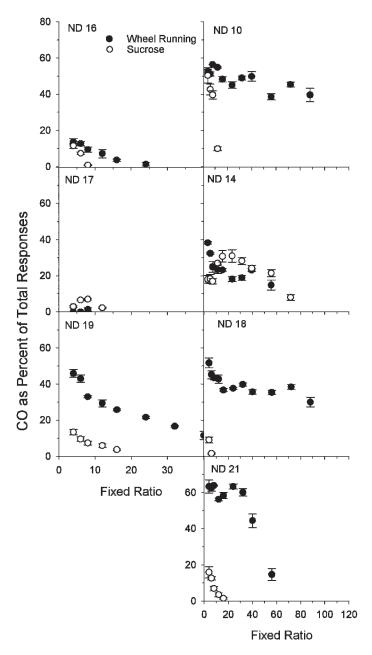


Fig. 9. Changeovers as a percentage of total responses as a function of fixed ratio schedule value for wheel running (filled circles) and sucrose (unfilled circles) reinforcement for rats ND 10, 14, 16, 17, 18, 19, and 21. Note that the scale on the abscissa is different for ND 10, 14, 18, and 21 because the data for these rats were extended over a much greater range than that for the other rats.

total responses when wheel running was the reinforcer (Belke & Belliveau, 2001; Belke et al., 2006), these data suggest that those observations arose because wheel running generates a lower local response rate.

Figure 10 shows mean response proportions on the increasing ratio requirement alternative, mean changeovers as a percent of total responses, mean total responses, and mean responses on the increasing and constant ratio

Table 1

Overall response rate (presses/min), local response rate (presses/minute), mean postreinforcement pause (s), and changeover rate (changeovers/min) for the concurrent FR 4 FR 4 condition with wheel-running and sucrose reinforcement.

		Wheel Run	ning	Sucrose						
Rat	Overall	Local	PRP	CO	Overall	Local	PRP	CO		
ND 2	9.1	90.3	23.6	16.6	30.9	101.9	5.7	14.3		
ND 3	12.5	116.0	17.3	29.9	68.2	200.9	2.4	25.7		
ND 5	13.4	143.9	16.6	45.5	26.2	116.0	6.6	28.5		
ND 7	3.5	20.6	58.7	0.6	69.1	221.7	2.3	15.2		
ND 8	11.4	94.4	17.6	14.9	31.9	151.5	5.8	24.6		
ND 9	13.2	60.6	13.6	18.4	39.7	123.9	4.1	30.2		
ND 10	5.4	21.3	33.3	11.2	12.8	21.3	7.8	10.8		
ND 11	17.3	59.6	10.0	26.5	20.1	70.3	8.4	9.0		
ND 13	8.4	133.0	26.8	2.0	40.7	131.0	4.0	18.1		
ND 14	9.2	51.2	21.7	19.5	26.0	61.3	5.1	11.1		
ND 16	8.4	80.0	25.6	11.2	24.7	93.2	6.3	11.0		
ND 17	5.0	148.6	47.2	0.0	49.8	228.3	5.1	6.4		
ND 18	10.1	33.6	16.6	17.3	118.4	296.5	1.2	25.6		
ND 19	11.9	47.8	14.8	21.8	53.1	131.0	2.6	17.2		
ND 21	8.8	32.4	19.2	20.7	45.1	133.9	3.5	20.3		

alternatives with sucrose and wheel-running reinforcement when the ratio requirement on the increasing alternative was 4, 6, 8, and 12 responses for the group. The upper left panel shows that as the ratio requirement increased, responses allocated to the increasing rate alternative decreased with sucrose and wheelrunning reinforcement. Initial allocations were equivalent, but when the ratio requirement was increased from 4 to 6 responses, responses allocated to this alternative decreased to a greater extent with sucrose as the reinforcer. With subsequent increases (i.e., 6 to 8 responses and 8 to 12 responses), decreases in responding were equivalent for both types of reinforcers leading to parallel lines describing response proportion decreases. The upper right panel shows that as the ratio requirement increased, changeovers as a percent of total responses decreased when sucrose was the reinforcer, but remained unchanged when wheel running was the reinforcer. The lower left panel shows that as the ratio requirement increased, total responses allocated increased with both reinforcers. This figure also shows that 0.1 ml of 7.5% sucrose generated more responses than did a 30-s opportunity to run.

Finally, the bottom right panel in Figure 10 shows that, for sucrose, responses allocated to the constant ratio alternative increased as responses on the increasing ratio alternative decreased—the changes are symmetrical sug-

gesting that they reflect reallocation. When the ratio requirements were equal, more responses were being allocated to the increasing ratio alternative; however, with the first increment to 6 responses, this difference was reversed. The functions for wheel running appear quite different. As the ratio requirement increased from 4 to 6 responses, responses allocated to the constant alternative increased; however, responses allocated to the increasing ratio alternative did not decrease. Instead, responses to this alternative remained relatively constant or increased slightly. With the next increment from 6 to 8 responses, responses allocated to the constant alternative continued to increase and responses to the increasing ratio alternative began to decrease. The increment from 8 to 12 responses led to further increments and decrements in responses to the constant and increasing ratio alternatives, respectively.

DISCUSSION

Conventional wisdom has it that on concurrent ratio schedules when the schedule requirements are equivalent, unlike concurrent interval schedules, the schedules do not operate to produce any specific allocation. As the schedule requirements diverge from equality by a factor of 2 or more, exclusive preference rapidly develops for the alternative with the lower ratio requirement (Davison &

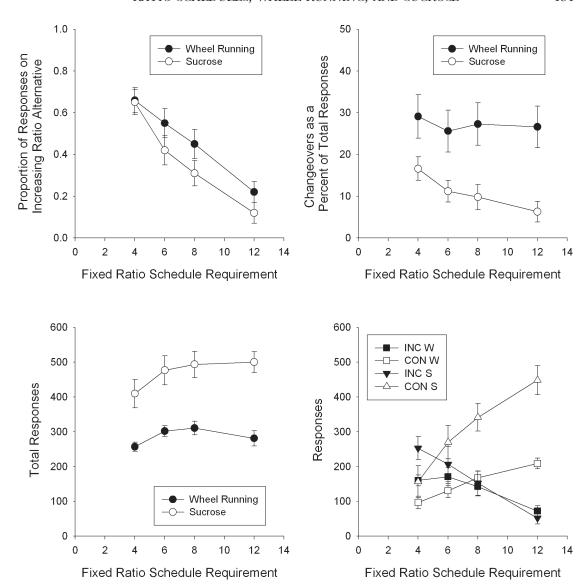


Fig. 10. The upper left panel depicts mean proportion of responses on the increasing ratio alternative with wheel running and sucrose reinforcement over ratio values of 4, 6, 8, and 12 responses. The upper right panel displays mean changeovers as proportion of total responses with wheel running and sucrose reinforcement over ratio values of 4, 6, 8, and 12 responses. The lower left panel shows mean total responses on both alternatives with wheel running and sucrose reinforcement over ratio values of 4, 6, 8, and 12 responses. The lower right panel portrays mean responses on the increasing (INC W) and constant (CON W) ratio alternatives with wheel running as the reinforcer and mean responses on the increasing (INC S) and constant (CON S) ratio alternatives with sucrose as the reinforcer.

McCarthy, 1988; Nevin, 1982). Results from the research literature (e.g., Herrnstein, 1970; Herrnstein & Loveland, 1975; MacDonall, 1988; Petry & Heyman, 1995) are the empirical basis for this understanding and this result is predicted by theories of choice such as melioration and maximization (Herrnstein,

1982; Herrnstein & Vaughan, 1980; Vaughan, 1981).

In the current study sucrose, but not wheelrunning reinforcement, conformed to this description of performance on concurrent ratio schedules. With wheel-running reinforcement, exclusive preference did not develop as rapidly as the ratio requirements began to differ in the majority of rats. In the most extreme cases, exclusive preference for the alternative with the lower ratio requirement did not develop even when the schedule values differed by a factor of 22 to 1. Although a few animals developed near-exclusive preference at lower ratios for wheel running than for sucrose reinforcement, for the majority of rats this criterion was met at a higher ratio with wheel-running reinforcement.

The data suggest that this difference between sucrose and wheel-running reinforcement arose due to several factors. Total responses generated increased as the ratio requirement increased for both reinforcer types; however, it appears that the additional responses may have been differentially distributed between the two alternatives. For sucrose, the allocation of responses as a function of changes in the ratio requirement suggests that responses were shifting away from the increasing ratio alternative and toward the constant ratio alternative. Additional responses generated did not affect this reallocation and exclusive preference rapidly developed. In contrast, with wheel-running reinforcement, as the ratio requirement increased, more responses were allocated to the constant ratio alternative; however, this was not accompanied by a decline in responses allocated to the increasing ratio requirement.

The procedure of raising the ratio requirement on the alternative with the higher initial preference raises the possibility that the rats had a bias toward that alternative which contributed to allocation of responses to that alternative as the ratio requirement was initially increased. Although this is possible, the ratio was increased on the same alternative for both reinforcer types and there is no reason to assume that there should be a bias with one, but not the other. Furthermore, in a preliminary unpublished experiment with wheel running as the reinforcer on both alternatives, the side on which the ratio schedule was increased was reversed and the effect was symmetrical. If side bias was playing a role, one would expect asymmetry. Side bias would lead to a higher ratio requirement to meet the 90% criterion when the ratio was raised on one alternative, but not on the other. Finally, the initial preferences, expressed as an absolute difference from 0.50, were not significantly correlated with the ratio that met the 90% criterion with wheel-running reinforcement, r(13) = -.32, the ratio that met the 90% criterion with sucrose reinforcement, r(13) = -.14, or the difference between the ratios that met the 90% criterion, r(13) = -.24.

The other substantive difference between wheel-running and sucrose reinforcement was that changeovers as a percent of total responses did not decrease with wheel running. With sucrose, as responses shifted toward the constant-ratio alternative, changeovers as a percent of total responses decreased as responding on the increasing ratio alternative decreased. Previous studies with food reinforcers have also found that changeover responses to the alternative with the lower rate of reinforcement typically decrease as preference for the higher rate alternative increases and approaches exclusive preference. However, with wheel-running reinforcement, there was a shift in preference toward the lower ratio alternative, but this shift in preference was not associated with a decline in changeovers. Changeovers to the higher-ratio alternative continued even though the ratio requirement for this alternative continued to increase and responses were reallocated to the constantratio alternative. Responding on the increasing-ratio alternative continued as the ratio requirement increased because changeover responses to this alternative were largely unaffected by continued increments in the ratio requirement. This could account for why exclusive preference for the constant-ratio requirement did not develop in some animals even though the ratio requirement on the other alternative was 22 times greater.

Another observation that might be important for explaining these data is that the rate of changeovers per unit time spent responding did not differ for the two types of reinforcers. In other words, per unit of time spent responding (excluding PRPs), changeover responses occurred just as frequently when wheel running was the reinforcer as when sucrose was the reinforcer. Although this rate of occurrence of changeovers did not differ, local response rates did. The local response rate generated by 0.1 ml of 7.5% sucrose was higher than that generated by a 30-s opportunity to run. In other words, per unit of time spent responding, sucrose generated more responses than did wheel running. Therefore, the higher percentage of total responses that were changeover responses when the reinforcer was wheel running occurred because wheel running generated fewer total responses, not more changeovers per unit time.

If the difference in response generation between a 30-s opportunity to run and a drop of 7.5% sucrose solution reflects a difference in value, then a 30-s opportunity to run would be equivalent to a drop of a lower percentage sucrose solution (see Belke & Hancock, 2003; Belke et al, 2006). Combined with the assumption that the rate of changeovers does not vary with value, this implies that for lower value reinforcers, a greater percentage of total responses will be changeover responses. As changeover responses come to constitute a higher percentage of total responses, this may enable a shift in response allocation to occur in response to changes in reinforcement contingencies without a decline in changeovers as occurred in the current study. The possibility that the important difference between wheel running and sucrose is one of value can be assessed by replicating this procedure across a range of sucrose concentrations that include low concentrations of sucrose (e.g., 2%)

As discussed in the introduction, another explanation for the lack of sensitivity to differences between reinforcement schedules has to do with inaccurate assignment of reinforcers to the alternative sources of reinforcement. Killeen and Smith's (1984) work suggested that this occurred due to the duration of time spent consuming a reinforcer. In the current study, the time period programmed for consumption of the sucrose reinforcer (2.5 s) was short relative to the time available for the rats to run (30 s). Furthermore, the average time following the termination of the programmed consumption period for sucrose before the rats began to lever press (i.e., the PRP) was also substantially shorter than the time following the termination of a running period before the rats begin to respond again. On average, the time between when a sucrose reinforcer was delivered and the next lever press was 7.2 s (2.5 s + 4.7 s)[median 4.7 s]. In contrast, the average time between when an opportunity to run began and the next lever press was 54.1 s (30 s + 24.1 s) [median 48 s].

The time differences between the reinforcers and the subsequent PRPs are sufficiently large

to warrant serious consideration as a factor in the observed differences with sucrose and wheel-running reinforcement. However, it should be noted that the reinforcer durations were the same for all rats, yet whereas most rats showed lower sensitivity to ratio differences with wheel running, a few showed lower sensitivity with sucrose, and a few showed approximately equivalent sensitivity with the two types of reinforcers. Nor is there any apparent relationship between PRP duration and the ratios at which rats met the 90% criterion for wheel running relative to sucrose reinforcement. Regardless, future research could assess this potential explanation better by programming equivalent reinforcer durations.

With respect to the Davison and Jenkins (1985) contingency discrimination model, it is possible that the increase in responses to the increasing ratio alternative when the ratio requirement was initially increased could have arisen due to the rats' inaccurate assignment of reinforcers. This would be consistent with the increases in, or lack of change in, relative response allocation to the increasing-ratio alternative observed in many rats as the ratio requirement initially increased. Similarly, the higher percentage of responses that were changeovers and the failure for changeovers to decrease as the ratio requirement increased could also have arisen due to confusion. However, not all data appear consistent with this model. First, the proportion of responses allocated to the increasing-ratio alternative decreased for both types of reinforcers as the ratio requirement initially increased. As such, relative response allocation appeared to be responsive to changes in ratio requirements with both types of reinforcers.

Second, for the rats whose responses shifted to the constant ratio alternative and then allocation leveled off and appeared relatively insensitive to further increases in the ratio requirement, responses on the increasing ratio alternative primarily were composed of change-over responses. If this was occurring due to inaccurate assignment of reinforcers to this alternative, one would expect there to be more responses that were not changeover responses.

What are the implications of these findings for theories of choice behavior? With sucrose reinforcement, responses shifted to the constant-ratio alternative and the percentage of total responses that were changeovers de-

creased as the ratio requirement increased on the other alternative. The covariance of these changes would be well described by a theory of choice that assumes that response allocation is a function of a single variable such as relative rate of reinforcement. In contrast, with wheelrunning reinforcement, responses shifted to the constant-ratio alternative, but changeovers as a percent of total responses were unaffected. Furthermore, for some animals, as the ratio requirement continued to increase, response allocation leveled out short of exclusive preference and remained relatively unaffected by further ratio increments. This pattern suggests that changeovers and responses other than changeovers were under the control of different variables and in this case, they did not covary. If this is the case, then describing these data would be problematic for any theory of choice that requires changeover responses to covary with changes in responses other than changeovers (e.g., melioration, maximization). Instead, a theory of choice would have to postulate separate sources of control over changeover responses and responses other than changeovers that could interact and either covary or not in order to be able to describe the data for both reinforcer types.

Finally, the findings from the current study provide an account for the lower sensitivity of response allocation to relative reinforcement rates compared to time allocation that was observed by Belke and Belliveau (2001). To the extent that responses on the alternative with the lower reinforcement rate were predominantly changeover responses followed by a quick return to the other alternative, the rats would allocate a single response and a fairly small amount of time to this alternative. On the alternative with the higher reinforcement rate, where the rat would make several successive responses, a low response rate would lead to a greater allocation of time than responses to this alternative. That is, time allocated to an alternative is greater when the time between responses is longer than when it is shorter. The combined effect of a low response rate when a rat was making successive responses on the higher-reinforcement rate alternative and the allocation of mostly changeover responses on the low-reinforcement rate alternative would be more extreme time than response ratios as the relative rates of reinforcement diverged from equality. This

difference would translate into greater sensitivity for time allocation than for response allocation. Removing changeover responses from both alternatives would correct for this effect by increasing response ratios.

In sum, when sucrose was the reinforcer, preference shifted as the ratio requirement on one alternative was initially incremented, and near-exclusive preference developed for the unchanged alternative when the difference was guite small. In contrast, when wheel running was the reinforcer, preference shifted as the ratio requirement increased, but unlike sucrose, this shift in preference was not accompanied by a decline in changeover responses. Consequently, near-exclusive preference did not develop until the difference in ratio schedule values was much greater, and sometimes not at all. This pattern of results on concurrent-ratio schedules has not been previously reported and contradicts the pattern of choice predicted by theories such as melioration and maximization (Herrnstein, 1982; Herrnstein & Vaughan, 1980; Vaughan, 1981).

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APPENDIX

Mean responses (resp), reinforcers (reinf), time (s), changeovers (CO), and revolutions (Revs) on the left (L) and right (R) alternatives from the three sessions that met the stability criteria for each concurrent FR FR schedule with wheel running (W) and sucrose (S) reinforcement for each rat. Time spent lever pressing is exclusive of reinforcer duration, but not postreinforcement pause duration. Wheel revolutions were zero in the sucrose conditions. Schedule (sched) values on the left and right alternatives are noted and the number of sessions to stability (SS) is also provided.

		Sch	ed	Res	sp	Rei	nf	Tin	ne	CO		Re	vs	
Rat		L	R	L	R	L	R	L	R	L	R	L	R	SS
ND 2	W	4	4	162	96	40.3	24.0	1000	698	24	24	751	496	13
		6	4	8	220	1.0	55.0	37	1834	2	3	16	1171	26
	S	4	4	180	153	45.0	38.3	306	350	23	23	0	0	15
		6	4	167	254	27.3	63.3	199	405	19	19	0	0	12
		8	4	194	281	24.0	70.3	202	434	19	18	0	0	11
	*	12	4	23	356	1.7	89.0	36	537	4	4	0	0	20
ND 3	W	4	4	251	44	62.7	10.7	1182	224	38	38	1224	179	19
		6	4	354	47	59.0	11.7	1177	304	35	35	1126	202	14
		8	4	387	73	48.3	18.0	1095	517	43	44	905	346	14
	C	12	4	21	236	1.3	59.0	51	1730	19	19	23	1090	18
	S	4	4	152	420	38.0	105.7	120	392	37	37	0	0	32
NID F	TAT	6	4	33	627	5.3	156.7	22	444	6	7	0	1000	11
ND 5	W	4	4	68	233	16.7	58.3	321	1032	47	48	290	1062	12
		6 8	4	68	$\frac{259}{257}$	10.7 7.3	64.7 64.3	219	1119 1276	54	54	205	1283	10
		12	4	61 71			71.3	165	1155	49 58	49 59	141 94	$1267 \\ 1342$	10 10
		16	4	58	$\frac{285}{263}$	5.3 3.3	65.7	129 106	1424	51	59 52	57	1045	16
		24	4	53	248	2.0	62.0	100	1563	49	50	30	1043 1072	10
	S	4	4	177	122	44.0	30.3	387	274	38	37	0	0	16
	3	6	4	108	247	17.7	61.7	166	493	32	32	0	0	19
		8	4	56	372	6.7	95.0	60	531	27	27	0	0	10
		12	4	30	556	2.3	139.0	28	464	18	19	0	0	14
ND 7	W	4	4	2	141	0.0	35.0	2420	1121	2	2	0	508	9
ND /	**	4	6	2	216	0.0	36.0	2441	1960	1	1	0	692	15
		4	8	6	251	1.3	31.3	2407	1890	3	3	28	640	11
		4	12	144	20	36.0	1.3	109	2279	7	7	681	28	14
		4	16	115	9	28.7	0.0	27	2662	5	6	551	0	10
	S	4	4	97	485	24.3	121.3	349	157	20	20	0	0	27
	5	4	6	143	641	35.7	106.7	359	160	20	20	0	0	11
		4	8	364	371	91.0	46.3	205	328	22	23	0	0	21
		4	12	431	76	107.7	6.0	44	549	10	10	0	0	17
		4	16	465	46	116.0	2.3	63	516	16	16	0	0	14
ND 8	W	4	4	72	217	17.3	54.3	310	1121	23	24	263	788	21
		6	4	29	180	4.7	45.0	145	1960	10	10	65	673	29
		8	4	48	154	5.7	38.3	359	1890	24	23	67	460	24
		12	4	11	116	0.3	29.0	88	2317	9	9	3	289	14
	S	4	4	245	113	61.0	28.0	416	240	29	29	0	0	25
		6	4	230	207	38.0	51.7	313	325	35	36	0	0	8
		8	4	76	489	9.3	122.3	77	453	18	17	0	0	29
		12	4	10	511	0.3	127.3	9	530	4	4	0	0	12
ND 9	W	4	4	233	73	58.3	17.7	924	398	46	46	1082	316	15
		6	4	166	174	27.7	46.3	423	972	38	37	501	846	23
		8	4	76	240	9.3	59.7	229	1306	38	38	157	1093	17
		12	4	29	266	2.3	66.3	88	1396	27	27	42	1119	17
		16	4	10	281	0.3	70.3	19	1434	9	9	6	1120	12
	S	4	4	285	130	71.0	32.3	393	230	51	51	0	0	10
		6	4	33	419	5.3	104.7	42	554	12	12	0	0	17
ND 10	W	4	4	82	110	20.3	27.0	1407	708	50	51	251	322	20
		4	6	120	153	29.7	25.3	1038	892	70	70	415	329	12
		4	8	142	131	35.3	16.0	788	1210	77	77	503	228	19
		4	12	176	129	44.0	10.3	599	1355	83	84	646	152	17
		4	16	185	92	46.3	5.0	393	1630	67	67	758	80	19
		4	24	118	53	30.3	2.0	617	1826	38	39	394	19	11
		4	32	142	63	35.3	1.3	367	2065	50	50	444	15	11

APPENDIX (Continued)

			ed	Resp		Rei	nf	Time		CO		Revs		
Rat		L	R	L	R	L	R	L	R	L	R	L	R	SS
		4	40	152	75	38.0	1.3	364	2006	57	57	475	16	17
		4	56	148	51	37.0	0.3	101	2251	38	39	485	5	26
		4	72	154	74	38.3	0.7	235	2189	52	52	469	8	13
	C	4	88	172	59	43.0	0.0	289	2006	45	46	484	0	32
	S	4 4	4 6	59 117	105	14.3 29.0	26.0 14.3	541 428	226 352	42	41	0	0	8
		4	8	156	87 77	38.3	9.3	344	420	44 46	44 46	$0 \\ 0$	0	14 13
		4	12	421	35	105.3	2.7	138	472	22	23	0	0	17
ND 11	W	4	4	104	225	25.7	56.0	757	385	$\frac{72}{74}$	73	471	1052	9
1,12 11	••	4	6	92	316	22.7	52.7	927	413	74	74	406	940	12
		4	8	162	255	40.3	31.7	642	794	87	87	736	555	12
		4	12	243	133	60.7	10.7	287	1154	77	77	1087	179	10
		4	16	275	29	68.3	1.3	71	1418	23	23	1221	23	36
	S	4	4	49	183	12.0	45.7	493	197	16	16	0	0	22
		4	6	239	108	59.7	18.0	165	467	10	10	0	0	24
		4	8	429	8	107.3	0.7	7	605	2	2	0	0	19
ND 13	W	4	4	248	2	62.0	0.0	1727	20	2	2	1202	0	22
		6	4	242	56	40.3	13.7	1295	666	22	22	795	263	8
		8 12	4 4	65 2	196 196	8.0 0.0	49.0 49.0	244 1	$1635 \\ 2043$	10 1	11 2	127 0	838 713	25 12
	S	4	4	251	169	62.7	42.0	343	264	29	30	0	0	12
	5	6	4	120	321	20.0	80.3	124	510	19	19	0	0	14
		8	4	99	445	12.3	111.3	86	474	15	15	0	0	12
		12	4	4	677	0.0	169.3	3	441	2	2	0	0	23
ND 14	W	4	4	117	142	29.0	35.3	773	904	49	49	362	449	8
		4	6	138	168	34.3	28.0	895	824	50	49	311	253	12
		4	8	167	141	41.7	17.7	1249	561	38	38	531	223	10
		4	12	221	88	55.3	7.0	1505	213	36	36	688	94	15
		4	16	244	36	61.0	2.0	1625	70	32	33	772	26	39
		4	24	249	34	62.3	1.0	1611	56	26	26	625	10	23
		4	32	231	27	57.7	0.0	1819	47	24	24	671	0	21
		$\frac{4}{4}$	40 56	217 183	30	54.3 45.7	0.0	$\frac{1857}{2107}$	43	28	29 14	535 373	0	11 20
	S	4	4	59	16 237	43.7 14.7	$0.0 \\ 52.3$	208	18 474	14 26	27	0	0	20 27
	3	4	6	97	213	24.0	35.3	343	379	28	28	0	0	9
		4	8	116	193	28.7	24.0	401	353	26	26	0	0	17
		4	12	164	190	41.0	15.3	477	235	48	48	0	0	10
		4	16	201	103	50.3	6.0	579	137	46	47	0	0	15
		4	24	184	86	46.0	3.3	519	105	42	43	0	0	11
		4	32	193	53	48.3	1.0	663	75	34	35	0	0	16
		4	40	292	57	73.0	1.0	601	52	41	41	0	0	15
		4	56	350	57	87.3	0.3	609	51	44	44	0	0	8
		4	72	388	19	97.0	0.0	566	23	16	16	0	0	19
ND 16	W	4	4	151	92	37.7	23.0	1169	571	17	17	691	426	17
		4	6	141	110	35.3	18.3	1235	706	16	16	690	380	10
		4	8	151	136	37.7	17.0	1355	564	14	14	729	356	34
		$\frac{4}{4}$	12 16	194 229	58 27	48.3 57.3	4.7 1.3	$1774 \\ 1733$	201 42	10 5	10 5	$880 \\ 1064$	85 26	32 8
		4	24	211	2	52.7	0.0	1953	20	1	1	961	0	30
	S	4	4	107	180	26.7	44.7	272	425	17	17	0	0	20
	~	4	6	268	78	66.7	12.7	558	118	13	13	0	0	12
		4	8	566	3	141.0	0.0	518	20	2	2	0	ő	33
ND 17	W	4	4	181	0	45.3	0.0	2168	0	0	0	697	0	11
		6	4	294	0	50.3	0.0	2050	0	0	0	848	0	12
		8	4	3	199	0.3	49.7	51	2039	1	1	7	920	21
	S	4	4	472	14	118.0	3.0	522	26	7	7	0	0	17
		6	4	394	112	65.7	27.7	356	140	17	16	0	0	36
		8	4	365	177	45.7	44.3	259	243	19	19	0	0	16
		12	4	33	470	2.3	117.3	45	523	6	6	0	0	24

TERRY W. BELKE

APPENDIX (Continued)

		Sch	ed	Res	sp	Rei	nf	Tin	ne	CO		Re	vs	
Rat		L	R	L	R	L	R	L	R	L	R	L	R	SS
ND 18	W	4	4	158	113	39.0	28.0	893	698	70	70	676	495	8
		6	4	152	170	25.3	42.3	608	963	73	73	430	730	20
		8	4	158	180	19.3	45.0	526	1127	73	74	324	785	11
		12	4	118	217	9.3	54.3	352	1316	72	73	149	863	12
		16	4	94	236	5.0	59.0	237	1448	60	61	82	1001	13
		24	4	81	204	3.0	51.0	330	1662	53	54	48	774	14
		32	4	75	179	2.0	44.7	207	1931	50	51	30	677	14
		40	4	57	191	1.0	47.7	98	2029	44	44	16	757	8
		56	4	57	224	0.7	56.0	65	1836	49	50	11	950	16
		72	4	59	205	0.0	51.3	108	1907	51	51	0	807	12
		88	4	45	204	0.0	51.0	66	1972	37	38	0	723	12
	S	4	4	77	696	19.0	174.0	80	312	35	35	0	0	13
		6	4	10	690	1.3	172.3	8	426	6	6	0	0	15
ND 19	W	4	4	175	116	43.7	28.7	889	539	67	67	623	392	13
		6	4	109	233	17.7	58.3	450	870	74	74	239	872	15
		8	4	79	280	9.7	70.0	282	927	60	59	149	1096	16
		12	4	82	287	6.3	71.7	303	953	54	54	96	1255	12
		16	4	66	312	3.7	77.7	178	966	49	49	52	1315	12
		24	4	51	316	2.0	79.0	159	984	40	40	32	1282	9
		32	4	36	311	1.0	77.7	148	1059	29	29	16	1137	21
		40	4	28	320	0.0	80.0	63	1110	20	20	0	1250	10
	S	4	4	450	60	112.3	14.7	469	89	34	34	0	0	20
		6	4	575	53	95.7	12.7	508	98	30	30	0	0	14
		8	4	192	364	23.7	90.7	207	387	21	20	0	0	13
		12	4	72	461	5.7	115.3	59	482	16	16	0	0	13
		16	4	17	405	0.7	101.0	12	603	8	8	0	0	20
ND 21	W	4	4	105	146	26.0	36.3	742	967	80	80	502	672	18
		4	6	131	180	32.7	29.7	880	839	97	97	633	564	16
		4	8	145	206	36.0	25.3	905	841	112	112	677	466	23
		4	12	136	177	34.0	14.3	1371	758	88	88	627	260	18
		4	16	143	237	35.7	14.7	1302	755	111	111	667	261	12
		4	24	166	175	41.3	7.0	1636	492	108	108	720	117	10
		4	32	192	161	48.0	4.7	1671	323	106	106	875	81	16
		4	40	195	72	48.7	1.3	1852	201	60	60	862	18	24
		4	56	203	18	50.7	0.0	1980	44	17	16	980	0	19
	S	4	4	105	316	26.0	79.0	118	442	34	33	0	0	10
		4	6	261	304	65.0	50.7	197	372	35	36	0	0	25
		4	8	339	195	84.7	24.3	311	207	18	18	0	0	10
		4	12	436	47	109.0	3.7	495	56	8	8	0	0	10
		4	16	429	8	107.3	0.3	553	13	3	3	0	0	14